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Population Dynamics and Reproduction of a *Musculium argentinum* (Bivalvia: Sphaeriidae) Population in Southern Chile, South America

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Abstract. The aim of the present study was to provide data about the population dynamics and reproductive traits of a *Musculium argentinum* (d'Orbigny, 1835) population inhabiting a channel next to the city of Lautaro in southern Chile. Results showed that *M. argentinum* size population structure varied during the study period, with brooding adults present throughout the year, with the highest frequencies in December 2002, and March, August and September 2003, producing offspring throughout the year. The smallest specimen brooding was 2.6 mm collected in May 2003 and the size of population first brooding corresponded to the 3.0–3.9 mm class size, collected in March 2003. *M. argentinum* at the study site is an ovoviviparous, iteroparous, sequential brooder, producing offspring throughout the year. These characteristics are attributed to the stable habitat.

INTRODUCTION

Sphaeriid clams are cosmopolitan and ubiquitous in their distribution. They are filter feeders and often play an important role in the dynamics of nutrient and energy cycling in freshwater bodies, i.e., streams and ponds (Wallace et al., 1977). Despite this importance in aquatic environments, relatively little is known about the life histories of sphaeriid clams, especially those from the Southern Hemisphere.

While the majority of marine bivalves are oviparous, with some notable exceptions (Mackie, 1984; Brusca & Brusca, 1990; Ponder, 1998) most freshwater bivalves, including families of the order Unionoida and the two veneroid families Sphaeriidae and Corbiculidae exhibit ovoviviparity and viviparity to various degrees.

Evolutionary aspects of the reproductive biology have been studied in limnic molluscs and put in a phylogenetic context in naiad bivalves (Unionoida) (Dillon, 2000; Graf, 2000; Graf & Ó'Foghil, 2000; Hoeh et al., 2001; Schwartz & Dimock, 2001); in finger nail clams and pill clams (Sphaeriidae) (Heard, 1977; Cooley & Ó'Foghil, 2000; Mansur & Meier-Brook, 2000; Korniushin & Glaubrecht, 2002). Studies conducted with freshwater clams, from the family Sphaeriidae provide an interesting perspective, since these clams are found in widely varying habitats. This is specially true for *Musculium*, which inhabits both permanent and temporary water bodies in the Northern Hemisphere, and which show differences in their reproductive traits, such as number of generations per year, bradictyc or tachytictic reproductive pattern among others.

Sphaeriidae is one of two families of freshwater bivalves represented in Chile (Parada & Peredo, 2002). The first record of *Musculium argentinum* (d'Orbigny, 1835) in continental Chilean waters was reported by Sobarzo et al. (2002). In view of the great variability in reproductive function and life cycles exhibited by *Musculium* populations inhabiting various habitats and the scarce, almost nonexistent studies on Sphaeriidae life cycles from the Southern Hemisphere, in South America in particular, in the present study, some aspects of the population dynamics and reproductive traits of a population of *M. argentinum* inhabiting a permanent freshwater body in the Southern Hemisphere, are described and compared with those of other populations of *Musculium* from the Northern Hemisphere.

MATERIALS AND METHODS

Musculium argentinum were collected monthly from September 2002 to September 2003 from the bank bed of a permanent channel which flows out from the Cautín river, next to the city of Lautaro, southern Chile (38°32′S;72°27O). At this point the channel is approximately 2 m wide, 0.2–0.6 m deep and has a moderately fast water flow (surface velocity of 0.2 m sec^{-1}). Most of the substrate at the collection site is composed of mud. Mean water temperature varied from 9.5°C in winter to 15°C in summer. The water is well-oxygenated (>77% saturated throughout the year) and a mean pH near neutrality (6.7). Samples were collected at random with a 15 × 10 cm standard grab,

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and specimens sifted through 1.0 mm sieves. Samples consisted of >100 clams.

Soft tissues of 10 individuals were histologically processed for light microscopy and examined to determine sex and gonad structure.

To determine the monthly population size structure of *Musculium argentinum*, the shell length (anterior to posterior dimension) was measured to the nearest 0.5 mm with a digital caliper for clams >2 mm long and with a stage-mounted micrometer under a dissecting microscope for clams <2 mm long.

Biometric parameters were determined and the following correlations defined: valve length (VL) vs. valve height (VH), VL vs. valve width (VW) and VL vs. specimen weight (SW).

To asses the reproductive status of the population, approximately 60 adults from each monthly sample were dissected to examine for the presence of embryos. From 8 adults, intramarsupial embryos were removed from each brooding sac in the inner demibranchs, and extramarsupial embryos in the mantle cavity, were counted and measured (length) to the nearest 0.01 mm with a stage-mounted micrometer (Wolfe 10×) under a dissecting microscope.

During 2002 spring months (November and December) and 2003 fall months (April and May) 18 brooding adults of sizes representative of the population were processed to estimate the number and size of intramarsupial and extramarsupial embryos. For intramarsupial embryos, four size classes were established: C1: 0.1–0.30 mm; C2: 0.31–0.6 mm; C3: 0.61–0.9 mm and C4: 0.91–1.2 mm. For extramarsupial embryos, all were larger than1.21 mm. The smallest individual with embryos and the smallest size class with equal or less than 50% of individuals brooding were determined each month.

RESULTS

Population Dynamics

The size of the specimens found during the study period ranged from 2.6 to 10.1 mm. The valve height (VH) ranged between 8.4 and 2.2 mm; valve width (VW) between 5.5 and 2.7 mm and wet weight between 5 and 21.6 mg. The biometric correlations VL vs. VH (R^2 = 0.9171), VL vs. VW (R^2 = 0.8656) and VL vs. VW (R^2 = 0.8277) are highly significant. The relation VL vs. number of brooding sacs in adults is not significant.

Monthly variations in adult population size structure between October 2002 and September 2003 did not show a definite tendency. However, small individuals (2.0–2.9 mm) were collected during December 2002, May, August and September 2003 (Figure 1).

Juveniles (<2 mm) were observed in November 2002, February, and May 2003 and in less abundance in December 2002, August and September 2003 (Figure 2).

Reproduction

Gonadal organization is shown in Figure 3. Male and female gametes can be seen within gonadal follicles. Male gametes are more abundant than female ones. Hermaphrodite individuals brood their embryos in the inner demibranchs. Monthly records show that more than 20% of adults have embryos in the brood sacs throughout the study period, reaching values close to 50% in December 2002, March, August and September 2003 (Figure 2).

Monthly records of brooding adults (18 individuals examined monthly) showed that the number of brooding sacs is variable, ranging from two to eight sacs in both inner demibranchs per individual, five being the maximum number of brooding sacs found in a single demibranch. There is no significant correlation between the number of brooding sacs and the size of adults (Figure 4).

The size of brooding sacs in an inner demibranch in the same individual is variable. The largest sac observed was 3.3 mm long and 1.8 mm wide. The smallest one was 0.57 mm long and 0.39 mm wide. Both values were registered in an adult 9.4 mm length in November 2002.

Table 1 shows data of number and size of intramarsupial and extramarsupial embryos from the brooding adults processed during spring 2002 (November and December) and fall 2003 (April and May). Results show that all brooding adults have sacs at different developmental stages. In individuals, the size of embryos within the same sac is almost the same. However, the size of embryos varies between brooding sacs showing that one adult is brooding embryos at different developmental stages simultaneously.

The smallest specimen with embryos (individual first brooding) observed was 2.6 mm in a specimen collected in May 2003. The smallest size class with more than 50% of brooding individuals was 3.0–3.9 mm in specimens collected in December 2002 (66.7%), March 2003 (100%) and July 2003 (80%).

DISCUSSION

The absence of correlation between valve length and number of brooding sacs observed, has been explained by the physical arrangement of offspring. Size limited brood capacity is common among species with hard exoskeletons such as molluscs (Bayne et al., 1983; Callow, 1983). Beekey & Hornbach (2004) reported in *Sphaerium striatinum* that brood size is constrained by the physical arrangement of offspring and the retention of extra-marsupial offspring. In *M. argentinum*, ab-

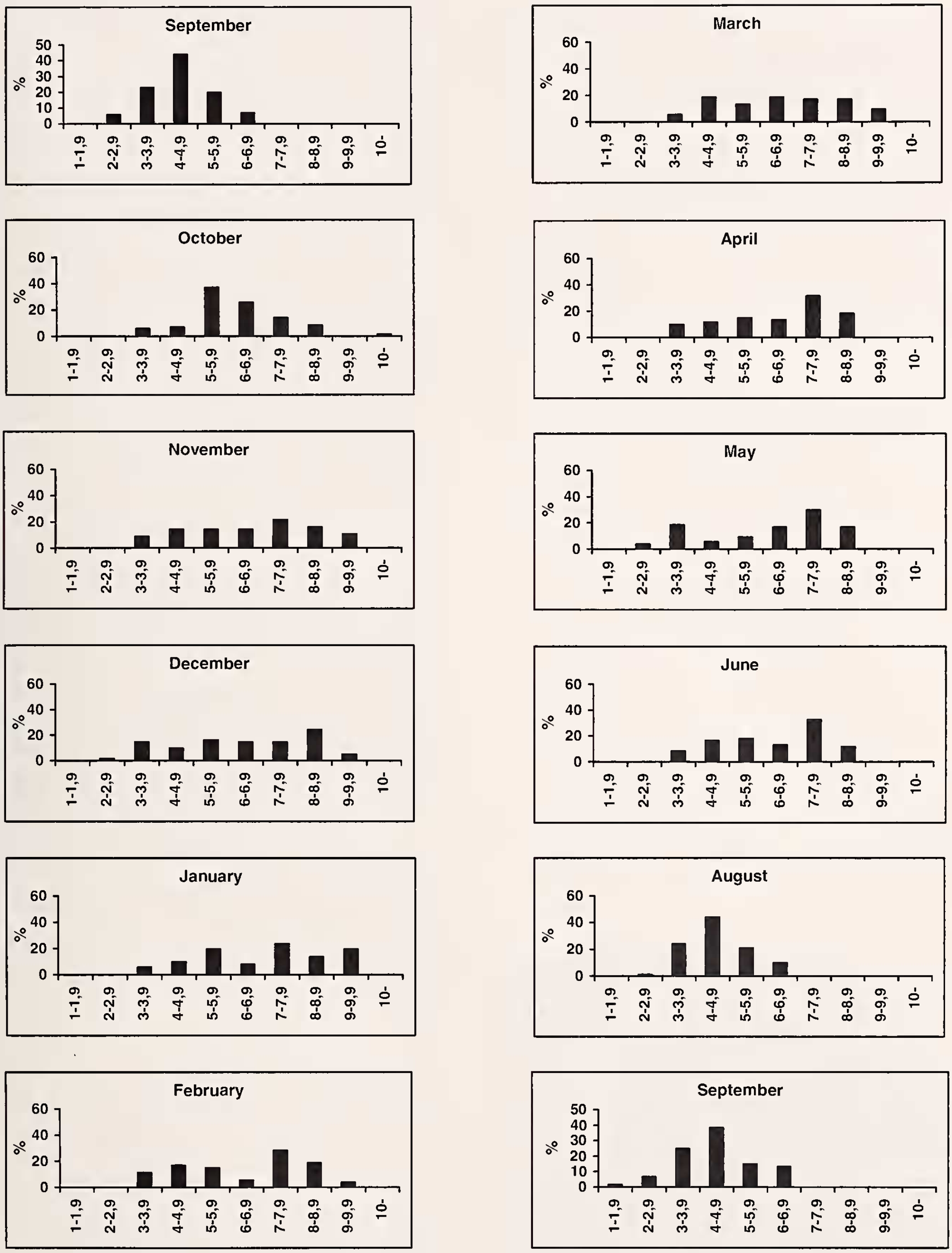

Figure 1. Monthly size structure of *M. argentinum* population at the study site during the study period.

sence of correlation between valve length and number of brooding sacs, can be explained just by the arrangement of offspring. (Table 1).

Like all Sphaeriids, *M. argentinum* is a simultaneous hermaphrodite and incubates eggs in the inner demibranchs within marsupial or brooding sacs. Our results indicate that the population dynamics of *M. argentinum* at the study site differs from that reported for

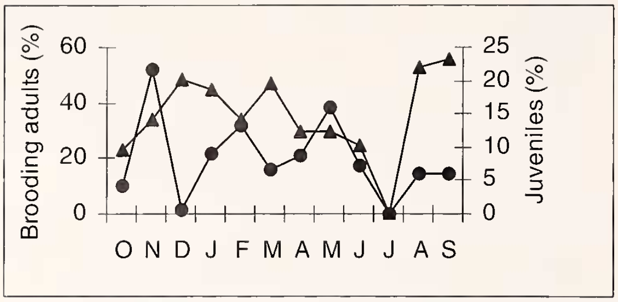

Figure 2. Monthly variation (%) of brooding adults and juvenile frequency (%) during the study period (▲: brooding adults %; ●: juveniles %).

other *Musculium* populations. In contrast to results reported by Mackie et al. (1976) in a *Musculium securis* (Prime) population, Morton (1985) for *M. lacustre*, Müller, Hornbach et al. (1991) for *M. partumeium* (Say) and O'Toole & Wilson (2001) for *M. lacustre* among others. *M.argentinum* at the study site, presents adults and juveniles throughout the study period.

In most of the studies carried on *Musculium* populations, definite spawning periods (juveniles or larvae release) have been reported, giving birth to cohorts. Hornbach et al. (1982) report two generations of clams were produced each year in a population of *Sphaerium striatinum* (Lamarck) in Ohio, with major recruitment occurring in April to early July. Morton (1985) and Hornbach et al.(1991) report two generations in a year (one spring and one fall generation) in *M. lacustre* in Hong-Kong and in ponds in Minnesota respectively. O'Toole & Wilson (2001) point out that *M. lacustre* produces just one generation in Citadel Pond, Dublin. Mouthon (2004) reports two spawning periods in *M. lacustre* in the Saône river at Lyon.

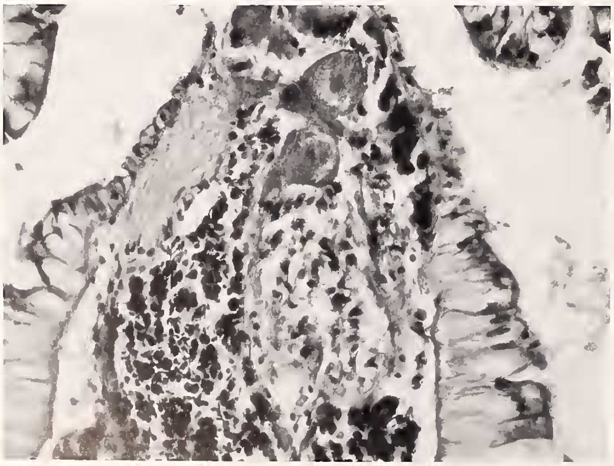

Figure 3. Microscopic organization of the gonad of *M. argentinum* showing the male (M) and the female (F) portion. ×1000.

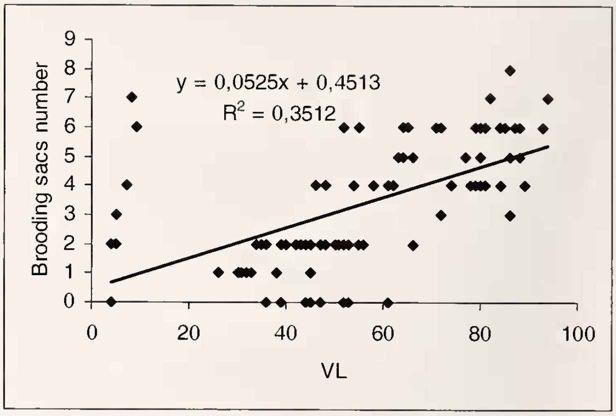

Figure 4. Brooding sacs number vs. adult valve length (mm).

According to our results, *M. argentinum* does not present definite spawning periods during the year. Therefore, *M. argentinum* would originate several cohorts in a year, November 2002, February, and May 2003 being the months with the highest number of juveniles collected in the substratum which were smaller, or of the same size than extramarsupial embryos (<2 mm). In this respect *M. argentinum* resembles *Sphaerium striatinum*, reported as a sequential brooder and producing offspring throughout the year (Beekey & Hornbach, 2004). This could be attributable to the stable habitat conditions, i.e., relative small temperature differences between winter and summer months, no great changes in hydrologic conditions (abundance and current flow) and in food supply (organic matter) throughout the year.

M. argentinum can be defined as ovoviviparous, in contrast to reports of Korniushin & Glaubrecht (2003), Hetzel (1993) for other Sphaeriids. Our definition is based on the fact that we did not observe in the sections examined the presence of epitheloidal cells- functional nutritive structures in the wall of brood sacs or any

Table 1

Size classes (C1–C4) and mean member of intramarsupial and extramarsupial embryos in brooding adults in spring and summer month of the study period.

	Spring 2002		Fall 2003	
	Nov	Dec	April	May
Adults n° processed	18	24	18	12
Adults size range (mm)	4.6–9.4	3.7–8.9	3.4–8.6	3.2–8.1
Mean number embryos: intramarsupial				
C1 (0.1–0.3 mm)	2	2.8	10.7	7.1
C2 (0.31–0.6 mm)	6.6	4.1	6.6	8.0
C3 (0.61–0.9 mm)	8.0	6.1	4.0	4.6
C4 (0.91–1.3 mm)	0.5	0.3	1.7	4.6
extramarsupial (>1.31 mm)	3.4	0.3	1.6	2.1

other cell or structure which could provide parental nutrients to the embryos. Therefore, embryo brooding in *M. argentinum* just provides parental care, so in a strict sense, this corresponds to ovoviviparity as has been reported for the great majority of Sphaeriids in agreement with Mackie's definition of ovoviviparity (Mackie, 1978) It is in disagreement with Meier-Brook (1970), Hetzel (1993) and Korniushin & Glaubrecht (2003) and others, who point out that Sphaeriidae qualify for the term eu-viviparous, on the basis that nutrients for embryonic development are mainly provided by the parental animal. At present, from our point of view, in Sphaeriidae and in *M. argentinum* in particular, the nutrition of embryos depends on the yolk stored in oocytes. Despite the small size of sphaeriid oocytes, due to the small size of specimens, including *M. argentinum*, the yolk contained in oocytes is sufficient to sustain embryo development. In addition, eu-viviparity would correspond to an anatomic connection between embryonic and maternal tissues, giving origin to the placenta, as present in some fishes, reptiles and mammals. Viviparity could be defined as when, in addition to parental care, embryo nutrition is provided by the parental animal by mean of secretory cells or any other way in which no tissue connection is involved. Posterior electron microscopy studies might clarify the nature of embryo nutrition in *M. argentinum*. *M.argentinum* has direct development, giving birth to small individuals (<2 mm). We did not observe any developmental stage that could correspond to a larval stage as reported by Hetzel (1993) who describes five larval stages in *M. lacustre* including sexually mature larvae.

The presence of brooding sacs in the inner demibranchs in the same individual with embryos in different development stages in *M.argentinum* corresponds to sequential brooding and represents an evolutionary progress of parental care, from synchrony without brood sac, synchrony with brood sac and sequential brooding with ontogenetically staggered brood sacs and brooded juveniles. This sequence of parental care may reflect selection for accelerated oogenic cycles, and early maturation which is a characteristic of several sphaeriid taxa (Cooley & Ó'Foghil, 2000). This is in accordance with the small size at which *M. argentinum* reaches sexual maturation.

M. argentinum has a small gonad as compared to Corbiculidae and *Eupera* and *Byssanodonta*, (Euperinae) which is in agreement with Dreher Mansur (1993). Examination of gonad sections revealed that the male portion of the gonad was at a more advanced stage of maturation than the female portion, which agrees with reports of Morton (1985) in *M. lacustre*. These observations differ from Mackie et al. (1976) who reported protogyny in *M. securis*, and who described gonads devoid of gametes during winter months. Despite the earlier maturation of the male portion of the gonads, final maturation and evacuation of gametes occur simultaneously. Simultaneous maturation of gametes also occurs in *M. partumeium* (Thomas, 1959) and *Sphaerium simile* (Say, 1817) (Zumoff, 1973). Within Sphaeriidae. *M. argentinum* showed gonads with mature gametes throughout the study period which included winter months. Therefore, *M. argentinum* is a simultaneous or functional hermaphrodite with active gonads throughout the year.

The presence of adults of *M. argentinum* throughout the study period which produce offspring throughout the year, could be indicative of iteroparity instead of semelparity as reported for other species of *Musculium* (Morton, 1985; O'Toole & Wilson, 2001; Mouthon, 2004). Our data therefore indicate the great variation in life history exhibited by Sphaeriids. This variation is determined by environmental conditions, reflecting a plasticity which has contributed to their cosmopolitan distribution. This variability in life history makes interpopulation comparisons difficult to interpret and also raises the probability that life cycles of many other species might be more variable than is at present appreciated.

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